

SALT MARSH LINKAGES TO PRODUCTIVITY OF PENAEID SHRIMPS AND BLUE CRABS IN THE NORTHERN GULF OF MEXICO

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Abstract

Secondary production derived from coastal marshes of the northern Gulf of Mexico exceeds that of other regions in the United States and is exemplified by large fishery catches of penaeid shrimps (*Farfantepenaeus aztecus*, *F. duorarum*, and *Litopenaeus setiferus* - 66 % of U.S.) and blue crabs (*Callinectes sapidus* - 25 % of U.S.). We believe that this production arises from coastal wetlands, and is driven by wetland geomorphology and hydrology resulting from the delta building and wetland loss cycles of the Mississippi River. Quantitative surveys document that high densities of shrimps and blue crabs directly use northern Gulf marsh surfaces. Manipulative experiments demonstrate that such marshes provide these fishery species with increased resources for growth and with protective cover to reduce predator-related mortality. Thus, access to the marsh surface is an important component in controlling the link between secondary productivity and coastal wetlands. Marsh access is influenced by tidal flooding patterns, amount of marsh/water edge, and extent of connections between marsh systems and the Gulf. Low-elevation Gulf marshes are flooded nearly continually during some seasons and are extensively fragmented; such characteristics provide maximum access. By contrast, U.S. Atlantic coast marshes have less fragmentation and less flooding. These geomorphic and hydrologic differences coincide with differences in secondary production between the regions, e.g., marsh-derived fishery production is lower on the Atlantic coast. Despite the linkage between coastal wetlands and secondary production, the current rapid loss of wetlands in the Gulf does not appear to be causing a decline, but instead is associated with an increase in fishery productivity. This paradox may be explained by changes in access and habitat function during areal loss of wetlands. Wetland loss is accompanied by increased marsh inundation and fragmentation, expansion of saline zones, and shortened migratory routes. These processes extend the utilization of remaining marsh and support temporary increases in secondary production.

1. Introduction

Shelf fisheries of the southeastern United States are characterized by estuarine dependency and an apparent linkage between coastal wetlands and fishery productivity. The Southeast Region's penaeid shrimp (mainly *Farfantepenaeus aztecus* and *Litopenaeus setiferus*) and blue crab (*Callinectes sapidus*) fisheries are prominent for both their magnitude and their apparent dependency on estuaries as nurseries. A positive correlation has long been recognized between area of coastal wetlands and the shrimp fishery landings (Turner 1977). This relationship suggests a marsh habitat-productivity link, but more direct evidence is required to conclusively document and explain how secondary production of fisheries is derived from coastal marshes.

Evidence for a direct link between coastal marsh habitat and fishery production may come in many forms. In general, the stronger the evidence, the more difficult it is to obtain. Simply documenting the presence of a species in a particular habitat may suggest linkage between this habitat and productivity of the species. Such documentation is relatively easy to obtain using qualitative sampling methods; however, this type of evidence is perhaps the weakest for establishing a habitat-productivity link. More convincing are data showing that a specific habitat, when compared with all other available habitats, contains highest densities of a species. This type of evidence can be obtained in interhabitat comparisons using quantitative sampling methods (Rozas and Minello 1997). Still stronger evidence for a habitat-productivity link requires documentation that a habitat provides one or more production-related necessities (e.g., food, protection, spawning area) for a species. Habitats where species have high survival and growth are most likely to be closely linked with high productivity. The most convincing evidence for a direct link between habitat and productivity would require a comparison of secondary productivity for a species among habitats. This type of analysis is difficult and often not practical. In general, the linkage between habitats and productivity should be demonstrated by direct evidence showing that a habitat both contains higher densities of a species than other habitats and provides essential requirements for survival and growth of that species.

Our objective in this paper is to review the evidence for direct linkages between salt marsh habitat of the northern Gulf of Mexico and productivity of three valuable fishery species, brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), and blue crab (*Callinectes sapidus*). We examine animal densities, growth, and mortality among marsh and other estuarine habitats. We discuss an emerging paradigm that stimulation of secondary production in northern Gulf fisheries is connected to wetland-loss processes. We explain how northern Gulf marshes may differ from southeastern Atlantic Coast marshes in derivation of secondary production. We examine the productivity responses of several decapod crustacea as affected by differing life history strategies, feeding, and predator avoidance behaviors. Taken as a whole, this body of information provides compelling evidence for a direct but variable connection between estuarine marsh habitat and productivity of brown shrimp, white shrimp, and blue crabs in the northern Gulf of Mexico.

2. Habitat-Related Densities

During their stay in Gulf coast estuaries, small juvenile penaeid shrimps and blue crabs are strongly associated with vegetation structure. Densities of these decapods are generally much more abundant in flooded emergent marsh vegetation or submerged grass beds than over nonvegetated sand or mud bottom. In a synthesis of published papers and unpublished reports on habitat use by nekton (restricted to quantitative enclosure samples), Minello (1999) calculated mean nekton densities in different estuarine habitats of Louisiana and Texas. Habitats examined included salt marsh edge, inner marsh, submerged aquatic vegetation (SAV), and shallow nonvegetated bottom. Overall mean densities were higher in marsh edge habitat than over shallow nonvegetated bottom for all three decapod species. Table 1 lists mean densities of penaeids and blue crabs from published studies that directly compared animal abundance in emergent marsh and over nonvegetated bottom.

TABLE 1. Mean densities (number per m²) of brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), and blue crabs (*Callinectes sapidus*) in marsh edge and shallow nonvegetated habitats of Texas and Louisiana. Densities are shown only for seasons when juveniles are abundant in estuaries. A paired-T test was used to compare densities between the two habitats. The data source is cited for each pair of means.

| | Marsh edge habitat | Nonvegetated bottom | Difference (Edge-NV) | P value (paired-T) |
|---------------------------------------|-----------------------|------------------------|-------------------------|-----------------------|
| Brown shrimp (spring-fall) | | | | |
| Minello and Webb (1997) | 12.0 | 3.3 | 8.7 | |
| Minello et al. (1991) | 9.2 | 0.4 | 8.9 | |
| Rozas and Minello (1998) | 4.5 | 0.5 | 4.0 | |
| Zimmerman and Minello (1984a) | 24.9 | 4.0 | 20.9 | |
| Zimmerman et al. (1989) | 9.6 | 1.1 | 8.5 | |
| Zimmerman et al. (1990a) | 5.0 | 1.7 | 3.3 | |
| Zimmerman et al. (1990b) | 5.0 | 1.2 | 3.7 | |
| Mean | 10.0 | 1.7 | 8.3 | 0.011 |
| White shrimp (summer and fall) | | | | |
| Minello and Webb (1997) | 26.7 | 6.0 | 20.7 | |
| Rozas and Minello (1998) | 4.2 | 0.0 | 4.2 | |
| Zimmerman and Minello (1984a) | 26.3 | 11.7 | 14.7 | |
| Zimmerman et al. (1989) | 4.2 | 0.3 | 3.9 | |
| Zimmerman et al. (1990a) | 1.6 | 1.5 | 0.1 | |
| Zimmerman et al. (1990b) | 4.4 | 0.8 | 3.6 | |
| Mean | 11.2 | 3.4 | 7.9 | 0.061 |
| Blue crab (all seasons) | | | | |
| Thomas et al. (1990) | 6.0 | 2.5 | 3.5 | |
| Minello and Webb (1997) | 6.4 | 0.7 | 5.6 | |
| Minello et al. (1991) | 4.6 | 0.0 | 4.6 | |
| Rozas and Minello (1998) | 10.7 | 0.3 | 10.4 | |
| Zimmerman and Minello (1984a) | 8.5 | 1.0 | 7.5 | |
| Zimmerman et al. (1990a) | 4.2 | 0.4 | 3.8 | |
| Zimmerman et al. (1990b) | 10.8 | 1.9 | 8.9 | |
| Mean | 7.3 | 1.0 | 6.3 | < 0.001 |

Overall mean densities of brown shrimp *F. aztecus* in Texas and Louisiana were estimated at 7.5 m^{-2} (SE 0.7) in *Spartina alterniflora* marsh edge habitat and 1.9 m^{-2} (SE 0.2) on nonvegetated bottom (Minello 1999). Most studies comparing brown shrimp abundance between these habitats reported densities of 3 to 13 m^{-2} in emergent marsh and $< 3.5 \text{ m}^{-2}$ over nonvegetated bottom (Table 1). The mean density of brown shrimp in SAV was 7.3 m^{-2} (SE 1.0) in Texas and Louisiana (Minello 1999). On the central Texas coast, Rozas and Minello (1998) found that densities of brown shrimp were similar in SAV (5.3 m^{-2} , SE 1.1) and marsh (5.0 m^{-2} , SE 0.8) in fall, but higher in SAV (11.3 m^{-2} , SE 1.3) than marsh (4.5 m^{-2} , SE 0.9) in spring.

White shrimp *L. setiferus* densities in Texas and Louisiana were reported by Minello (1999) to be 5.5 m^{-2} (SE 1.0) in *S. alterniflora* marsh edge compared with 1.2 m^{-2} (SE 0.2) on nonvegetated bottom; and in most comparisons shown in Table 1, white shrimp densities were higher in marsh than over nonvegetated bottom. Densities were similar in the two habitats only in one study (Zimmerman et al. 1990a), where overall white shrimp densities were relatively low ($< 2 \text{ m}^{-2}$). Minello (1999) reported low overall densities of white shrimp in SAV (0.5 m^{-2} , SE 0.1), but few studies have directly compared densities in SAV and emergent marsh edge. Zimmerman et al. (1990b) compared marsh edge with *Vallisneria* and *Halodule* habitats, and densities were about five times higher in the marsh. In a study on the central Texas coast, mean densities of white shrimp were twice as high in *Spartina alterniflora* marsh edge as in mixed aquatic beds of *Halodule wrightii* and *Ruppia maritima* (4.2 m^{-2} , SE 0.9 vs 1.9 m^{-2} , SE 1.5), although these differences were not statistically significant (Rozas and Minello 1998).

Young blue crabs *C. sapidus* appear to be closely associated with vegetation in estuaries. In most published reports, densities in marsh habitat are about an order of magnitude greater than on shallow nonvegetated bottom (Table 1). Overall mean densities in Texas and Louisiana were 6.2 m^{-2} (SE 0.7) in *S. alterniflora* marsh edge, 0.9 m^{-2} (SE 0.1) on nonvegetated bottom, and 5.0 m^{-2} (SE 1.2) in SAV (Minello 1999). Where direct measurements were compared between different contiguous vegetated habitats, results are conflicting. Rozas and Minello (1998) found higher mean densities of blue crabs in marsh edge than SAV both in fall (11.1 m^{-2} , SE 0.9 vs 7.5 m^{-2} , SE 1.4) and in spring (10.3 m^{-2} , SE 1.0 vs 2.5 m^{-2} , SE 0.3). In contrast, blue crab densities from *Halodule* beds in Christmas Bay, Texas were higher than in nearby marsh edge in 7 of the 12 months sampled (Thomas et al. 1990).

In most comparisons of nekton densities between salt marsh and nonvegetated bottom, only the marsh edge was sampled. Animal densities along the marsh edge are generally much higher than in marsh located farther from the water-marsh interface (Baltz et al. 1993, Peterson and Turner 1994, Kneib and Wagner 1994, Minello et al. 1994). For example, overall mean densities from the studies examined by Minello (1999) were much higher in marsh-edge than inner-marsh ($>5 \text{ m}$ from shoreline) habitat (white shrimp: 5.5 m^{-2} , SE 1.0 vs 1.6 m^{-2} , SE 0.9; brown shrimp: 7.5 m^{-2} , SE 0.7 vs 0.4 m^{-2} , SE 0.2; blue crab: 6.2 m^{-2} , SE 0.7 vs 0.5 m^{-2} , SE 0.1). Therefore, nekton densities reported for marsh-edge habitat cannot be extrapolated to the entire marsh surface. However, marsh-edge habitat is extensive in Louisiana and Texas where much of the salt marsh is highly reticulated due to coastal submergence and marsh fragmentation.

3. Marsh-Related Growth

Food is a principal attractant leading to estuarine habitat selection (Boesch and Turner 1984, Kneib 1984, Minello and Zimmerman 1991, McTigue and Zimmerman 1991). Penaeid shrimps generally feed by browsing and digging through surface sediments. Both juvenile white shrimp and brown shrimp are omnivorous and known to eat epiphytic algae, marsh detritus, and animal material in the laboratory (Condrey et al. 1972, Gleason and Zimmerman 1984, McTigue and Zimmerman 1991), but species-specific differences in feeding have been documented. Initial evidence that juvenile brown shrimp and white shrimp feed directly upon marsh infauna was obtained from an unpublished laboratory feeding experiment using marsh sediment cores. Thirty-six cores (10 cm dia. x 5 cm ht.) were collected from a *Spartina alterniflora* marsh on Galveston Island and maintained as microcosms in 25-cm (ht.) PVC sleeves. The cores were held under laboratory conditions of 25 °C, 20‰ salinity, and alternate cycles of 12 h light and 12 h dark. Individual juvenile brown shrimp and white shrimp (28 mm in total length) were placed in 24 cores (12 cores with each species) as treatments. Twelve cores without shrimp served as a control. After 5 d, each core was sieved through a 500- μ screen; and remaining peracarids, annelids, and mollusks were identified and counted. Feeding was quantitatively inferred from differences in numbers of infauna between treatment and control cores. Results of this depletion experiment indicate that marsh annelids (mainly spionids and capitellids) and peracarids (mainly tanaidaceans and amphipods) were readily eaten by the juvenile shrimps. Brown shrimp and white shrimp significantly reduced the numbers of peracarid crustaceans and annelid worms in marsh sediments, and brown shrimp ate significantly more than white shrimp (Fig. 1, ANOVA, $P < 0.05$). Additional experiments reported by McTigue (1993) and McTigue

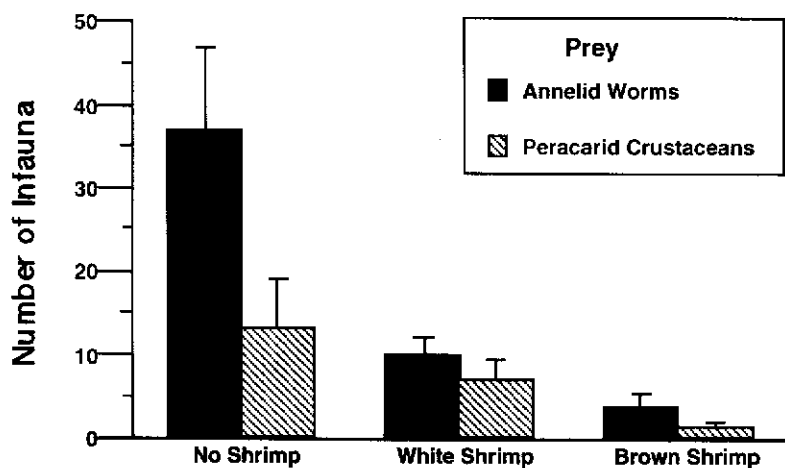


Figure 1. Feeding by brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) on annelid worms and peracarid crustaceans in sediments from a subsiding salt marsh on Galveston Island, Texas. Mean number + 1 SE of infauna removed by shrimp from 78 cm² x 15 cm cores of marsh sediment (n = 12 cores per treatment).

and Zimmerman (1998) confirmed the basic differences in feeding habitats of brown shrimp and white shrimp. Brown shrimp are more effective at removing infauna from sediments and appear to be obligate carnivores that depend on dense numbers of infauna found on the marsh surface. In contrast, white shrimp are less effective at removing infauna from sediments; this species is truly omnivorous and depends more on plant resources than brown shrimp (McTigue 1993).

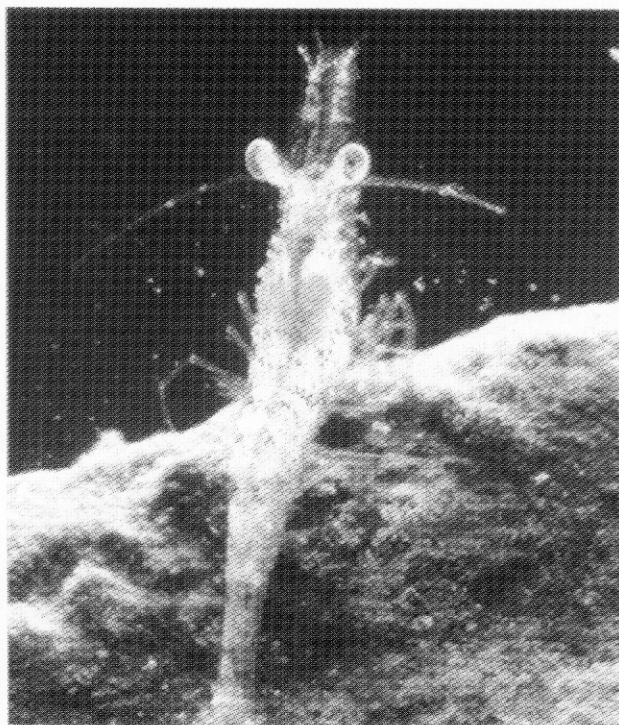


Figure 2. A newly metamorphosed juvenile white shrimp, *Litopenaeus setiferus*, approximately 23 mm in length, feeding on epiphytic algae attached to smooth cordgrass (*Spartina alterniflora*) culm (photograph by R. Zimmerman).

Growth studies also indicate differences in trophic requirements of brown shrimp and white shrimp. Both species may benefit from feeding on the marsh surface, but brown shrimp productivity appears to be more closely linked with marsh infauna. Brown shrimp will feed on salt marsh detritus and epiphytes, but assimilation was not detected from these treatment diets (Gleason 1986). Juvenile brown shrimp seem to depend on infaunal worms for growth, and densities of these prey organisms are relatively high on the marsh surface (Zimmerman et al. 1991, Whaley 1997). Brown shrimp held in cages showed significantly higher growth rates when they had access to the marsh surface (as high as 1.4 mm d^{-1}) than when they were restricted to subtidal bottom (Zimmerman and Minello 1984b). Simultaneous caging of juvenile white shrimp revealed no difference in growth between marsh and open-water habitats. White shrimp attain better growth on

diatoms or epiphytes and some natural animal dietary component (perhaps mysids or copepods) that has yet to be identified (McTigue and Zimmerman 1998). Kneib and Knowlton (1995) and Kneib (1997) suggest that white shrimp may be important predators on early life history stages of daggerblade grass shrimp *Palaemonetes pugio*. The ability of white shrimp to exploit plant resources also is suggested by rapid growth observed in pond studies. In ponds without macrophytes that were fertilized to promote phytoplankton, growth rates were reported for juvenile white shrimp of 2.1 mm d⁻¹ (Johnson and Fielding 1956) and 2.3 mm d⁻¹ (Wheeler 1968). By comparison, brown shrimp in Wheeler's (1968) experiments grew at 1.0 mm d⁻¹ in fertilized ponds and 1.1 mm d⁻¹ in unfertilized ponds.

Thomas (1989) tested dietary habits of juvenile blue crabs in natural microcosm cores similar to those described above. Her results demonstrate that blue crab diets are different from those of juvenile shrimps. Post megalopae juvenile blue crabs fed significantly more on epiphytic algae and peracarid crustaceans than on annelid worms. In a caging study conducted on open bay bottom, Minello and Wooten (1993) also found that small juvenile blue crabs (12-17 mm CW) did not appear to feed on infauna. Infaunal densities in this experiment were low, but positive growth of enclosed crabs was measured. Other investigators have documented plant and animal material in guts of blue crabs, and their studies suggest an ontogenetic change in diet to more carnivory as individuals grow (Alexander 1986, Laughlin 1982, Ryer 1987). Rosas et al. (1994) noted that, in general, as blue crabs increase in size, plant matter, sediment, and unidentified animal residues in guts decrease in favor of increases in molluscs and crustaceans. Fitz and Wiegert (1991) found a predominance of feeding on fishes and non-portunid crabs (*Uca* sp., grapsid and xanthid crabs) by large blue crabs in Georgia marshes, and West and Williams (1986) and Schindler et al. (1994) reported that adult blue crabs actively fed upon molluscs such as *Littoraria* sp. on the marsh surface. Ryer (1987) found that blue crab guts contained more food at high tide than at any other period of the tidal cycle and suggested this as evidence that blue crabs foraged in intertidal marshes.

4. Benefits of Marsh-Surface Access to Feeding

A major function of salt-marsh habitat is to serve as a feeding area for opportunistic estuarine species, and there is evidence that this function varies regionally. Historically, salt marshes were thought mainly to contribute to detritus-based food webs by outwelling plant debris into estuaries and coastal areas downstream of marshes (Nixon 1980, Peters and Schaaf 1991). Such indirect use of plant production from Atlantic coast marshes is consistent with relatively high elevations (limiting accessibility for nekton) and large tidal amplitudes (providing energy to transport detritus). But in the northern Gulf of Mexico, direct use of the marsh surface appears to be widespread, fostered by extended tidal flooding associated with low marsh elevations and a narrow tidal range. Greater access to the marsh surface gives young fishery species an opportunity to feed on an abundance of infauna, epiphytic and edaphic algae, and small primary consumers that provide high-quality food necessary for rapid growth. Microalgal trophic pathways have been described from Gulf marshes (Sullivan and

Moncreiff 1990), and the relative importance of algal versus detrital pathways is likely controlled by marsh-surface availability (McIvor and Rozas 1996). Importantly, regional differences in secondary productivity are influenced by differences in opportunistic feeding behavior among estuarine species (Kneib 1995). Differences in productivity and the resulting fishery yields of estuarine-dependent species such as penaeid shrimps and blue crabs are in part due to species-specific abilities to utilize marsh habitat for feeding.

5. Salt Marshes and Mortality of Shrimps and Crabs

Vegetated estuarine habitats also affect productivity of shrimps and crabs by providing cover or refuge and reducing mortality. A major cause of mortality for penaeid shrimps and blue crabs is predation by estuarine fishes (Minello and Zimmerman 1983, Wilson et al. 1987, 1990, Minello et al. 1989, Heck and Coen 1995). Juvenile blue crabs also suffer significant mortality from cannibalism by larger crabs (Orth and van Montfrans 1982, Hines and Ruiz 1995). Mortality due to predators appears to be lower within vegetated estuarine habitats in comparison with nonvegetated bottom. Laboratory experiments have shown that the structure of salt marsh vegetation reduces feeding rates of some estuarine fishes on brown shrimp (Fig. 3) and blue crabs (Minello and Zimmerman 1983, Thomas 1989, Minello et al. 1989). Seagrass structure has also been shown to reduce predation rates on a variety of crustacean prey (Coen et al. 1981, Heck and Thoman 1981, Main 1987) including juvenile blue crabs (Orth and van Montfrans 1982, Orth et al. 1984, Thomas 1989). Predator-induced mortality, however, also depends on the suite of predators present within habitats, and laboratory experiments do not always reflect mortality in the field. Tethering experiments are designed to incorporate differences in trophic webs among habitats in addition to differences in environmental characteristics other than structure. For example, shallow water, that may be associated with some vegetated habitats, has been shown to reduce predation and mortality of blue crabs (Ruiz et al. 1993, Dittel et al. 1995, Hines and Ruiz 1995). Field experiments with tethered blue crabs and brown shrimp prey have shown that mortality is reduced in seagrass and marsh habitats compared with nonvegetated bottom (Heck and Thoman 1981, Wilson et al. 1987, 1990, Minello 1993, Heck et al. 1994). All of these data, therefore, support the hypothesis that vegetated habitats such as salt marshes and seagrass beds reduce predator-related mortality of crustaceans like penaeid shrimps and blue crabs.

The protective value of vegetated habitats varies. Intertidal salt marsh is not always flooded and available for exploitation by shrimps and crabs; thus, regional differences in tidal dynamics can affect the protective value of salt marshes. In the northern Gulf of Mexico, flooding durations during spring and fall are extensive (Rozas and Reed 1993, Minello and Webb 1997). During these seasons, salt marshes may function quite similarly to seagrass in these estuaries (Rozas and Minello 1998). There is also some indication that vegetated habitats with very high densities of plants offer less protective cover, because thick mats of roots and rhizomes prevent burrowing in the substratum (Wilson et al. 1987). Both blue crabs and penaeid shrimps often burrow during the day, and this

behavior reduces mortality caused by both predators (Fuss 1964, Fuss and Ogren 1966, Minello et al. 1987) and by temperature extremes (Eldred et al. 1961, Aldrich et al. 1968).

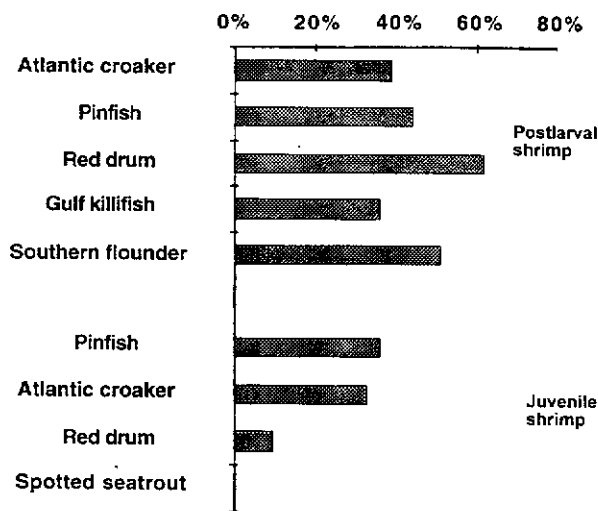


Figure 3. Reduction in feeding rates on brown shrimp due to vegetation. Experiments comparing feeding by various fish predators between bare sand and vegetated habitats were conducted in laboratory microcosms using planted *Spartina alterniflora* and postlarval shrimp (Minello et al. 1989) or simulated vegetation and juvenile shrimp (Minello and Zimmerman 1983).

In addition to predator-related mortality, both penaeid shrimps and blue crabs suffer mass mortality from periodic detrimental physical conditions in the estuary such as freezing weather (Gunter 1941, Gunter and Hildebrand 1951, Dahlberg and Smith 1970) and anoxic water (Gunter 1942, May 1973, Turner and Allen 1982, Turner et al. 1987). Habitats that function to protect shrimps and crabs from predators do not necessarily provide refuge from these sources of mortality. Deep water and an appropriate substratum for burrowing may be important habitat characteristics for reducing mortality from low temperatures (Eldred et al. 1961, Aldrich et al. 1968).

Regional differences in the value of salt-marsh habitats in reducing mortality may be related to differences in tidal dynamics, marsh morphology, trophic structure, and climate. Earlier we discussed the benefits to shrimps and crabs of access to the marsh surface for feeding. The increased marsh access prevalent along the Gulf coast should also provide increased protective benefits. These benefits, however, may be reduced in part by increased predation pressure in Gulf estuaries. Heck and Wilson (1987) and Heck and Coen (1995) found that predation on crabs in vegetated habitats was higher at lower latitudes and higher along the Gulf coast than along the Atlantic coast. The dominant predators may also vary regionally. Fish predators are generally considered the most significant sources of mortality for shrimps and crabs in Gulf estuaries (Minello et al. 1989, Heck and Coen 1995). In Chesapeake Bay, however, Hines and Ruiz (1995) attributed almost all mortality of tethered juvenile blue crabs to cannibalism by larger crabs. In addition, climatic differences between much of the U.S.

Atlantic coast and the Gulf coast may affect the protective value of different habitats. Deep-water habitats with soft substrata may be especially valuable in climates and seasons where temperatures drop to lethal levels for crabs and shrimps. In these situations, seagrasses in deep waters may provide protection from both predators and the physical environment.

6. Seasonal Differences in Salt-Marsh Value

Direct benefits of marsh habitat to transient juveniles of fishery species may depend upon the seasonal timing of larval recruitment to the estuary. Flooding of marsh surfaces in the Gulf varies seasonally, and benefits can be proportionately greater for species that immigrate into the estuary when marshes are most accessible. Postlarval brown shrimp are at their peak abundance during the spring and fall (Baxter and Renfro 1967), coinciding with tidal high water periods that inundate salt marshes extensively (Rozas and Reed 1993, Minello and Webb 1997). Juvenile white shrimp are abundant during fall when marshes are flooded; however, postlarvae mainly recruit in the summer when intermediate water levels persist. Blue crab megalopae recruit into Gulf estuarine habitats in summer and fall (Rabalais et al. 1995), but juveniles overwinter in the estuary. During winter, marshes are relatively inaccessible, and the lowest water levels of the year occur. We suggest that seasonal hydrology affects marsh use and related benefits to production among these three species. On the basis of these seasonal-use patterns, brown shrimp should accrue the most benefit from salt-marsh habitats followed by white shrimp and blue crabs.

Abundances of infaunal prey organisms such as annelid worms and crustaceans in Gulf estuaries are usually more numerous in salt-marsh habitat than on subtidal bottom during most months (Fig. 4). Population levels of infauna vary seasonally, and densities are generally highest in late winter months when predator densities are low (Flint and Yount 1983, Zimmerman et al. 1991, Whaley 1997). This peak in infauna throughout the estuary coincides with the arrival of brown shrimp postlarvae in early spring. Infaunal densities decline to summer low levels, presumably due to predation, by the time white shrimp postlarvae arrive in Gulf estuaries. Blue crab megalopae arrive in the summer and fall, but juveniles overwinter in the estuary and are present in marshes throughout the year (Thomas et al. 1990, Rabalais et al. 1995, Rozas and Minello 1998). Subadult and adult blue crabs also use salt marshes (Thomas et al. 1990, Fitz and Wiegert 1991). This extended period of marsh use by all life-cycle stages for blue crabs contrasts with the seasonally limited use by juvenile penaeid shrimps. Energy derived from foraging in marshes by shrimps is used mainly for growth, while benefits for blue crabs are to growth and reproduction.

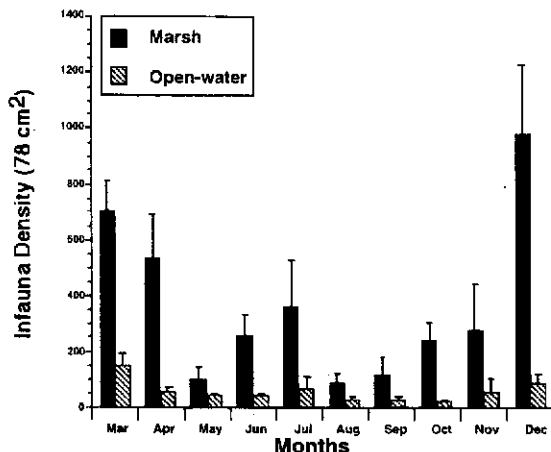


Figure 4. Seasonal densities of infaunal prey (annelid worms and peracarid crustaceans) in a subsiding marsh and adjacent subtidal habitat from 78 cm² x 15 cm cores of sediment taken at Galveston Island in the northern Gulf of Mexico (Zimmerman et al. 1991). Mean and standard error, n = 8 cores in each habitat monthly from 1985 through 1988.

7. Fishery Trends

The fisheries for brown shrimp and white shrimp are the largest crustacean fisheries in the United States, and they are centered in the northern Gulf of Mexico. Because the production of these species appears to depend on coastal wetlands, the high rates of wetland loss in the region are a matter of concern for fishery managers (Condrey and Fuller 1992). The brown shrimp fishery is the largest shrimp fishery in the Gulf of Mexico, and parent stocks of this species have remained relatively stable since 1960 (Eldridge 1988, Nance et al. 1989, Klima et al. 1990, Nance 1993). However, landings of brown shrimp doubled between 1960 and 1991 (Fig. 5) coinciding with increased fishing effort. Using virtual population analyses, the number of shrimp recruits was calculated for each of 31 years of catch data (1960 to 1991) where size composition and fishing effort are known. This analysis showed that recruitment to the brown shrimp fishery increased significantly through this period to historic high levels in 1991, and that increased landings are not solely due to increased fishing effort. The current dominance of brown shrimp in the fishery is recent; white shrimp dominated landings in the Gulf from the late 1800s to 1950 (Condrey and Fuller 1992). The white shrimp fishery in the Gulf is still large, however, and landings more than doubled between 1960 and 1986 (Fig. 5, Nance et al. 1989, Nance 1993). Recruitment of white shrimp has also increased significantly, with the largest increase between 1984 and 1986. Both of these shrimp fisheries have been considered fully exploited at least since the early 1970's, providing further evidence that increases in the Gulf landings of brown shrimp and white shrimp are caused by increases in recruitment. Blue crab landings in the Gulf of Mexico have increased similarly to brown shrimp and white shrimp since 1960

(Fig. 5). No trend in recruitment is known. Another large crustacean fishery, and the third largest shrimp fishery in the Gulf of Mexico, is pink shrimp *F. duorarum*. In contrast to other shrimp species, the principal nurseries for pink shrimp in the Gulf are seagrasses in South Florida and South Texas, and Gulf landings of pink shrimp have not exhibited a steady pattern of increase during the past three decades.

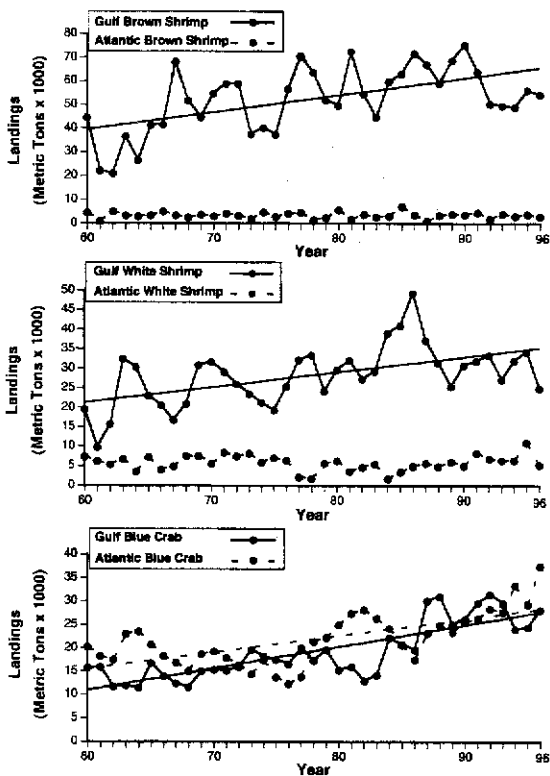


Figure 5. United States southeastern Atlantic and Gulf of Mexico landings of brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*) and blue crab (*Callinectes sapidus*) from 1960 through 1996 (U.S. National Marine Fisheries Service catch statistics data compiled by the Southeast Fisheries Science Center, Miami, Florida). Regression lines denote significant trends.

Fisheries for brown shrimp, white shrimp, and blue crabs of the southeastern U.S. Atlantic coast are associated with salt-marsh dominated estuaries (Weinstein 1979, Wenner and Beatty 1993). However, landings of shrimp per unit area of salt marsh are more than three times higher in the Gulf than the Atlantic (Table 2). In the Atlantic, penaeid shrimp fisheries fluctuate annually like those of the Gulf, but Atlantic landings have not increased significantly since 1960 (Fig. 5), and no trend in recruitment is known. Unlike the Gulf, the southeast Atlantic shrimp fishery has always been dominated by white shrimp. Blue crab landings along the Atlantic have increased similarly to those in the Gulf (Fig. 5). Also, fishery-independent surveys of abundances of juvenile blue crabs appear within the same order of magnitude between the two regions (Heck and Coen

1995). These similarities suggest that regional differences in marsh habitat are not a major factor influencing blue crab production. The northern extension of blue crab landings to the upper mid-Atlantic coast, where penaeid shrimp fisheries are inconsequential, suggests that blue crabs tolerate a wider range of environmental conditions than penaeid shrimps.

TABLE 2. Shrimp fishery landings (kg) per ha of salt marsh in Gulf of Mexico and Atlantic states where brown shrimp (*Farfantepenaeus aztecus*) and white shrimp (*Litopenaeus setiferus*) predominate. The total area of salt marsh (ha), portion of total U.S. salt marsh area (%), total shrimp landings (metric tons, all species combined-*F. aztecus*, *L. setiferus*, and *F. duorarum*), and landings per ha of marsh are given for each state and region.

| State | Marsh (ha) | % of U.S. | 1996 Shrimp Landings | |
|-------------------------|------------|-----------|----------------------|-------|
| | | | Metric tons | kg/ha |
| Louisiana | 697,223 | 40.4 | 36645.6 | 52.5 |
| Texas | 174,862 | 10.1 | 28057.6 | 160.4 |
| Northeast GOM Subtotal | 872,085 | 50.5 | 64703.2 | 74.1 |
| South Carolina | 148,072 | 08.6 | 2433.5 | 16.4 |
| North Carolina | 086,116 | 05.0 | 2391.2 | 27.7 |
| Georgia | 078,548 | 04.5 | 2637.1 | 33.5 |
| South Atlantic Subtotal | 312,736 | 18.1 | 7461.8 | 23.8 |
| Five State Total | 1,184,821 | 68.6 | | |
| Overall U.S. Total | 1,728,190 | | | |

(Marsh acreage recalculated from: Coastal Wetlands of the United States: an accounting of a valuable natural resource. 1991. U.S. Dept. of Commerce, NOAA/NOS and Dept. of the Interior, U.S. F. W. S. 59 p.; with conversion of acres = 0.4047 hectares)

8. Relationship of Marsh Submergence to Productivity

Increasing yields of brown shrimp and white shrimp over the past 30 years in the northern Gulf of Mexico are correlated with high rates of subsidence and loss of marsh habitat, and there is evidence that wetland-loss processes may have stimulated secondary productivity of these fishery species (Nance et al. 1989, Zimmerman et al. 1991). With high rates of marsh submergence, protection and feeding benefits of nursery habitat are modified for transient juveniles through:

- 1) Extension of the saline zone inland, providing more salt-marsh nursery area;
- 2) Lengthened duration of marsh inundation, allowing more time to feed and seek refuge among plant cover;
- 3) Greater accessibility to marsh habitat from open water due to increased edge; and
- 4) Shorter migration routes from the sea to inland marshes.

Relationships between submergence and productivity can also be seen by examining annual changes in sea level. Morris et al. (1990) reported that annual growth of *Spartina alterniflora* in South Carolina varies by a factor of two and correlates positively with anomalies in mean sea level. Moreover, commercial landings of shrimp and menhaden

of the southeast Atlantic and central Gulf of Mexico are directly correlated with sea level. Childers et al. (1990) noted that relationships between annual water levels and shrimp harvest in the Gulf were curvilinear. Low catches occurred in years of low or high water levels and high catches were in years with intermediate water levels. Low water was attributed to drought. We note that low catch in high water years can be attributed to high rainfall in which lower salinities restrict the area of suitable nursery habitat for young shrimp.

9. Regional Differences

Juvenile shrimps, blue crabs, and other transient marine taxa exhibit regional differences in direct use of the marsh surface, and these differences appear related to regional differences in hydrology and marsh inundation (Zimmerman et al. 1991, Rozas 1995). Northern Gulf salt marshes support densities of penaeid shrimps and blue crabs (Zimmerman and Minello 1984a, Rozas and Reed 1993) that are an order of magnitude greater than densities in East coast marshes (Hettler 1989, Mense and Wenner 1989, Fitz and Wiegert 1991, Kneib 1991, Rozas 1993). We attribute higher densities in Gulf marshes in part to longer inundation times that increase accessibility of subsiding marshes. We also suggest that the differences between Gulf and Atlantic fishery landings, which are largest in brown shrimp, followed by white shrimp and then blue crab, may be attributed to influences of marsh geomorphology and tidal hydrology.

As sea level rises in Gulf of Mexico salt marshes, especially during periods of accelerated rise, marshes are submerged, and habitat characteristics change (Deegan and Thompson 1985, Conner and Day 1987, Wells 1987, DeLaune et al. 1989). The classic configuration of a stable marsh along the Atlantic coast with its dendritic creeks disappears. In the Gulf, the marsh landscape becomes fragmented as interior ponding occurs (Turner and Rao 1990, Turner 1997), and patches of marsh become interspersed within subtidal areas of open water (Fig. 6). This condition creates more edge interface between salt marsh and open water (Browder et al. 1985) resulting in greater direct accessibility of the marsh surface for transient aquatic fauna.

The connections we have outlined between production of fisheries and marsh loss also can be related to characteristics of marsh building and wetland loss cycles of the Mississippi River delta. Rates of sedimentation and subsidence during the aging process of deltaic lobes strongly influence the biological characteristics of marshes (Neill and Deegan 1986, Rejmanek et al. 1987, Reed and Cahoon 1992). For example, recently-formed Atchafalaya delta marshes are dominated by strong riverine inflow, active delta building, and low subsidence rates (Wells 1987, DeLaune et al. 1987). These accreting Atchafalaya marshes, although inundated frequently, may be unavailable to some estuarine consumers due to low salinities; although Castellanos (1997) reports relatively high standing stocks of blue crabs here. Madden et al. (1988) emphasize that secondary production from the building Atchafalaya delta is driven by seasonal input of river-borne nutrients and sediments. By contrast, in an older deltaic system there is little direct river input, and marshes such as those in the lower Barataria Basin are rapidly subsiding and deteriorating (Sasser et al. 1986). These submerging marshes provide additional sources

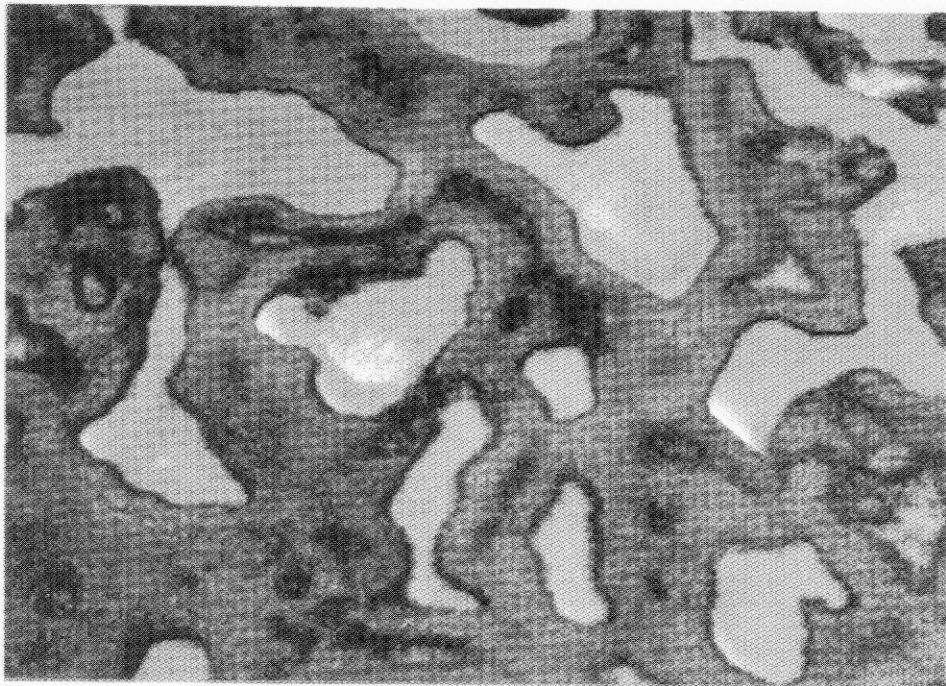


Figure 6. Highly fragmented salt marshes in the northern Gulf of Mexico provide maximum access to the marsh surface for fishery species. Oblique aerial photograph encompassing approximately 3 ha of marsh in Galveston Bay (taken by T. Minello).

of carbon and nitrogen exported to surrounding open waters (Feitjtel et al. 1985, DeLaune et al. 1989). In the Barataria system, marsh utilization by transient marine consumers is favored by higher salinities and organic detritus eroded from old marshes. Deegan and Thompson (1985) reported the mean density of fishes (sampled with otter trawls) to be more than an order of magnitude greater in Barataria Bay ($0.32 \text{ individuals m}^{-2}$) than in Atchafalaya Bay ($0.02 \text{ individuals m}^{-2}$).

10. Future Trends

The characteristics of drowning marshes, i.e., expansion inland, extended duration of flooding, more edge, and higher erosion rates, may benefit nursery function and enhance fishery production only over the short-term. For example, one model (Browder et al. 1989) suggests that marsh conversion to open water in Barataria Bay will soon reach a point beyond which fisheries will decline due to a reduction in the total amount of marsh area. The implication is that, over the long term, high yields supported by marsh submergence can be maintained only as long as marsh area lost is regenerated elsewhere. Nationally, Dahl and Johnson (1991) reported that areal losses of saline marshes have been more than replaced by encroachment into freshwater wetlands.

Future rates of eustatic sea level rise may further change marsh habitats nationwide and affect derived secondary production. The potential for greater production from marshes of Georgia and the Carolinas rests upon whether submergence will have the same affect as in the Gulf. In the northwestern Gulf, the relatively large marshes of the Chenier plain (Gosselink et al. 1979, DeLaune et al. 1983) are also susceptible to future submergence. Therefore, accelerated rates of sea level rise may stimulate estuarine-dependent fisheries even more widely than at present. But, as noted above, enhanced yields can continue only as long as drowning marshes are replaced by inland progression of saline wetlands. Eventual nationwide losses of total marsh area are highly probable as more barriers are constructed to protect inland areas. Saline marshes would be caught between the rising sea and protected shorelines. In this case, continual decline in marsh area would offset the functional benefits of submergence for fishery species. As a consequence, coastal fisheries may respond to sea-level rise rates predicted by global warming (Armentano et al. 1988) with short-term productivity increases, such as we believe have occurred in the Gulf shrimp fishery, that are unsustainable in the long-term (Browder et al. 1989, Condrey and Fuller 1992).

11. Conclusions

Patterns of estuarine utilization indicate that the productivity of brown shrimp, white shrimp, and blue crabs is linked to salt marshes. Indeed, investigators have amply demonstrated that estuarine wetlands provide the young of these fishery species with an abundant source of food that supports rapid growth, in addition to protective cover that reduces mortality from predators. Correspondingly, the largest area of emergent wetlands, including salt marshes and the largest crustacean fisheries in the U.S. are located in the northern Gulf of Mexico.

The linkages between salt-marsh wetlands and fishery productivity, however, are complex and varied. The importance of salt-marsh availability as nursery habitat has only been recognized fully within the last decade. The availability of coastal marshes to fishery species is determined by tidal flooding patterns, the amount of marsh/water edge, and the extent of connections between interior marsh and the sea. Within the northern Gulf of Mexico, low-elevation marshes are flooded almost continually during some seasons and are extensively fragmented, providing maximum access for young shrimp and blue crabs. By contrast, marshes along the southeastern U.S. Atlantic coast are less inundated and have relatively little marsh/water edge. Densities of transient aquatic species using the marsh surface also differ; the densities in the Gulf are generally an order of magnitude greater than those on the Atlantic coast. We now believe that these differences in wetland availability and degree of use are at least partially responsible for higher production and higher landings of some estuarine-dependent species in the Gulf of Mexico as compared with the U.S. Atlantic.

Overlying the concept of relative wetland value based upon hydrology is modification due to wetland loss. Salt-marsh loss is occurring throughout the southeastern U.S., but the highest rates are in the northern Gulf of Mexico. Because of the proposed linkage between wetlands and fishery production, we might expect estuarine-dependent fisheries to decline

as spatial extent of marsh habitat diminishes. In the northern Gulf of Mexico, however, recruitment and landings have increased for brown shrimp and white shrimp over the last 20 to 30 years. By comparison, landings of these species have remained stable along the U.S. Atlantic coast where wetland loss is relatively low. We are left with an interesting paradox — that of increased shrimp fishery production correlated with the loss of nursery habitat. The explanation appears to be related to the process of wetland loss. As the total area of coastal marsh decreases, inundation of existing marshes increases, fragmentation and habitat edge increase, zones of saline and brackish wetlands expand, and connections with the sea are shortened. We believe that the wetland loss process increases the availability and functional value of remaining marsh to transient fishery juveniles, which supports short-term increases in secondary production such as in shrimp. In the long-term, however, these enhanced levels of secondary productivity are not sustainable; continued wetland loss will eventually overtake short-term benefits derived from habitat loss, and future declines in estuarine-dependent shrimp production are unavoidable.

Brown shrimp, white shrimp, and blue crab are opportunistic species. Their productivity does not entirely depend on salt-marsh habitat, because they also occur in estuaries dominated by mangroves and SAV. However, in coastal areas with abundant salt marsh, the productivity of these fishery species appears to depend upon their ability to use the marsh surface directly as determined by hydrographic and geomorphic conditions. This interaction, of productivity and salt marsh habitat, also depends on the life history and behavioral characteristics of the different fishery species. Together, these factors can account for both regional and intraspecific differences in secondary productivity. In the northern Gulf of Mexico, brown shrimp production appears to have benefited the most from this salt marsh relationship, followed by white shrimp and blue crab.

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13. Literature Cited

- Aldrich, D. V., C. E. Wood and K. N. Baxter. 1968. An ecological interpretation of low temperature responses in *Penaeus aztecus* and *P. setiferus* postlarvae. *Bulletin of Marine Science* 18:61-71.
- Alexander, S. K. 1986. Diet of the blue crab, *Callinectes sapidus* Rathbun, from nearshore habitats of Galveston Island, Texas. *Texas Journal of Science* 38:85-89.
- Armentano, T. V., R. A. Park and C. L. Cloonan. 1988. Impacts on coastal wetlands throughout the United States. Pages 87-149 in J. G. Titus, editor. Greenhouse effect, sea level rise and coastal wetlands. EPA-230-05-86-013, U.S. EPA, Office of Policy, Planning and Evaluation, Washington, District of Columbia, USA.

- Baltz, D. M., C. Rakocinski and J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* **36**:109-126.
- Baxter, K. N. and W. C. Renfro. 1967. Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. *Fishery Bulletin, U.S.* **66**:149-158.
- Boesch, D. F. and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* **7**:460-468.
- Browder, J. A., H. A. Bartley and K. S. Davis. 1985. A probabilistic model of the relationship between marshland-water interface and marsh disintegration. *Ecological Modeling* **29**:245-260.
- Browder, J. A., L. N. May, A. Rosenthal, J. G. Gosselink and R. H. Baumann. 1989. Modeling future trends in wetland loss and brown shrimp production in Louisiana using thematic mapper imagery. *Remote Sensing of the Environment* **28**:45-59.
- Castellanos, D. L. 1997. Nekton use of submerged aquatic vegetation, marsh and shallow unvegetated bottom in a Louisiana tidal freshwater ecosystem. Thesis, University of Southwestern Louisiana, Lafayette, Louisiana, USA.
- Childers, D. L., J. W. Day and R. A. Muller. 1990. Relating climatological forcing to coastal water levels in Louisiana estuaries and the potential importance of El Nino-Southern Oscillation events. *Climate Research* **1**:31-42.
- Coen, L. D., K. L. Heck and L. G. Abele. 1981. Experiments on competition and predation among shrimps of seagrass meadows. *Ecology* **62**:1484-1493.
- Condrey, R. E. and D. Fuller. 1992. The U.S. Gulf shrimp fishery. Pages 89-119 in M. H. Glantz, editor. *Climate variability, climate change and fisheries*. Cambridge University Press, England.
- Condrey, R. E., J. G. Gosselink and H. J. Bennett. 1972. Comparison of the assimilation of different diets by *Penaeus setiferus* and *Penaeus aztecus*. *Fishery Bulletin, U.S.* **70**:1281-1292.
- Conner, W. H. and J. W. Day. 1987. The ecology of Barataria Basin, Louisiana: an estuarine profile. U.S. Fish and Wildlife Service Biological Report **85**(7.13).
- Dahl, T. and C. Johnson. 1991. Wetlands: status and trends in the conterminous United States, mid-1970s to mid-1980s. Report to Congress, U.S. Department of the Interior, Fish and Wildlife Service, Washington, District of Columbia, USA.
- Dahlberg, M. D. and F. G. Smith. 1970. Mortality of estuarine animals due to cold in the Georgian coast. *Ecology* **51**:931-933.
- Deegan, L. A. and B. A. Thompson. 1985. The ecology of fish communities in the Mississippi River deltaic plain. Pages 35-56 in A. Yanez-Arancibia, editor. *Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration*. UNAM Press, Mexico City, Mexico.
- DeLaune, R. D., R. H. Baumann and J. G. Gosselink. 1983. Relationships among vertical accretion, coastal submergence and erosion in a Louisiana Gulf coast marsh. *Journal of Sedimentary Petrology* **53**:147-157.
- DeLaune, R. D., T. C. Feijtel and W. H. Patrick. 1989. Nitrogen flows in Louisiana gulf coast salt marsh: spatial considerations. *Biogeochemistry* **8**:25-37.
- DeLaune, R. D., C. J. Smith, W. H. Patrick and H. H. Roberts. 1987. Rejuvenated marsh and bay-bottom accretion on the rapidly subsiding coastal plain of the U.S. Gulf coast: a second order effect of the emerging Atchafalaya Delta. *Estuarine, Coastal and Shelf Science* **25**:381-389.
- Dittel, A. I., A. H. Hines, G. M. Ruiz and K. K. Ruffin. 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bulletin of Marine Science* **57**:902-916.
- Eldred, B., R. M. Ingle, K. D. Woodburn, R. F. Hutton and H. Jones. 1961. Biological observations on the commercial shrimp, *Penaeus duorarum* Burkenroad, in Florida waters. Florida State Board of Conservation, Professional Paper Series **3**:1-139.
- Eldridge, P. J. 1988. The southeast area monitoring and assessment program (SEAMAP): a state-federal-university program for collection, management and dissemination of fishery-independent data and information in the southeastern United States. *Marine Fisheries Review* **50**:29-39.
- Feijtel, T. C., R. D. DeLaune and W. H. Patrick. 1985. Carbon flow in coastal Louisiana. *Marine Ecology Progress Series* **24**:255-260.
- Fitz, H. C. and R. G. Wiegert. 1991. Utilization of the intertidal zone of a salt marsh by the blue crab *Callinectes sapidus* - density, return frequency and feeding habits. *Marine Ecology Progress Series* **76**:249-260.
- Flint, R. W. and J. A. Younk. 1983. Estuarine benthos: long-term community structure variations, Corpus Christi Bay, Texas. *Estuaries* **6**:126-141.

- Fuss, C. M., Jr. 1964. Observations on burrowing behavior of the pink shrimp, *Penaeus duorarum* Burkenroad. *Bulletin of Marine Science, Gulf and Caribbean* **14**:62-73.
- Fuss, C. M. and L. H. Ogren. 1966. Factors affecting activity and burrowing habits of the pink shrimp, *Penaeus duorarum* Burkenroad. *Biological Bulletin* **130**:170-191.
- Gleason, D. F. 1986. Utilization of salt marsh plants by postlarval brown shrimp: carbon assimilation rates and food preferences. *Marine Ecology Progress Series* **31**:151-158.
- Gleason, D. F. and R. J. Zimmerman. 1984. Herbivory potential of postlarval brown shrimp associated with salt marshes. *Journal of Experimental Marine Biology and Ecology* **84**:235-246.
- Gosselink, J. G., C. L. Cordes and J. W. Parsons. 1979. An ecological characterization study of the Chenier Plain coastal ecosystem of Louisiana and Texas, Volumes. 1-3. U.S. Fish and Wildlife Service Report FWS-OBS-78/9, 10 & 11.
- Gunter, G. 1941. Death of fishes due to cold on the Texas coast, January, 1940. *Ecology* **22**:203-208.
- . 1942. Offatts Bayou, a locality with recurrent summer mortality of marine organisms. *American Midland Naturalist* **28**:631-633.
- Gunter, G. and H. H. Hildebrand. 1951. Destruction of fishes and other organisms on the South Texas coast by the cold wave of January 28-February 3, 1951. *Ecology* **32**:731-36.
- Heck, K. L., L. Coen, S. G. Morgan and R. K. Zimmer-Faust. 1994. Recruitment and habitat utilization by the blue crab *Callinectes sapidus*: the importance of juvenile nursery habitats to the fishery. Marine Fisheries Initiative (MARFIN) final report to NOAA National Marine Fisheries Service, St. Petersburg, Florida, USA.
- Heck, K. L. and L. D. Coen. 1995. Predation and the abundance of juvenile blue crabs: a comparison of selected East and Gulf Coast (USA) studies. *Bulletin of Marine Science* **57**:877-883.
- Heck, K. L. and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* **53**:125-134.
- Heck, K. L. and K. A. Wilson. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology* **107**:87-100.
- Hettler, W. F. 1989. Nekton use of regularly flooded salt marsh cordgrass habitat in North Carolina, USA. *Marine Ecology Progress Series* **56**:111-118.
- Hines, A. H. and G. M. Ruiz. 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bulletin of Marine Science* **57**:884-901.
- Johnson, M. C. and J. R. Fielding. 1956. Propagation of the white shrimp, *Penaeus setiferus* (Linn.) in captivity. *Tulane Studies in Zoology* **4**:175-190.
- Klima, E. F., J. M. Nance, E. X. Martinez and T. Leary. 1990. Workshop on definition of shrimp recruitment overfishing. NOAA Technical Memorandum NMFS-SEFC-264.
- Kneib, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries* **7**:392-412.
- . 1991. Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Marine Ecology Progress Series* **75**:29-38.
- . 1995. Behaviour separates potential and realized effects of decapod crustaceans in salt marsh communities. *Journal of Experimental Marine Biology and Ecology* **193**:239-256.
- . 1997. The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology: an Annual Review* **35**:163-220.
- Kneib, R. T. and M. K. Knowlton. 1995. Stage-structured interactions between seasonal and permanent residents of an estuarine nekton community. *Oecologia* **103**:425-434.
- Kneib, R. T. and S. L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* **106**:227-238.
- Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bulletin of Marine Science* **32**:807-822.
- Madden, C. J., J. W. Day and J. M. Randall. 1988. Freshwater and marine coupling in estuaries of the Mississippi River deltaic plain. *Limnology and Oceanography* **33**:982-1004.
- Main, K. L. 1987. Predator avoidance in seagrass meadows: Prey behavior, microhabitat selection, cryptic coloration. *Ecology* **68**:170-180.
- May, E. B. 1973. Extensive oxygen depletion in Mobile Bay, Alabama. *Limnology and Oceanography* **18**:353-366.

- McIvor, C. and L. P. Rozas. 1996. Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the southeastern United States. Pages 311-334 in K. F. Nordstrom and C. T. Roman, editors. *Estuarine shores: evolution, environments and human alterations*. John Wiley & Sons, New York, New York, USA.
- McTigue, T. A. 1993. Trophic roles in juvenile *Penaeus aztecus* Ives and *Penaeus setiferus* (Linnaeus) in a Texas salt marsh. Dissertation. Texas A&M University, College Station, Texas, USA.
- McTigue, T. A. and R. J. Zimmerman. 1991. Carnivory versus herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). *Journal of Experimental Marine Biology and Ecology* **151**:1-16.
- . 1998. The use of infauna by juvenile *Penaeus aztecus* Ives and *Penaeus setiferus* (Linnaeus). *Estuaries* **21**:160-175.
- Mense, D. J. and E. L. Wenner. 1989. Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus*, in tidal marsh creeks near Charleston, South Carolina. *Estuaries* **12**:157-168.
- Minello, T. J. 1993. Chronographic tethering: a technique for measuring prey survival time and testing predation pressure in aquatic habitats. *Marine Ecology Progress Series* **101**:99-104.
- . 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of Essential Fish Habitat. Pages 43-75 in L. Benaka, editor. *Fish habitat: essential fish habitat and habitat rehabilitation*. American Fisheries Society Symposium **22**.
- Minello, T. J. and J. W. Webb, Jr. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Marine Ecology Progress Series* **151**:165-179.
- Minello, T. J., J. W. Webb, R. J. Zimmerman, R. B. Wooten, J. L. Martinez, T. J. Baumer and M. C. Pattillo. 1991. Habitat availability and utilization by benthos and nekton in Hall's Lake and West Galveston Bay, NOAA Technical Memorandum, NMFS-SEFCS-275.
- Minello, T. J. and R. B. Wooten, Jr. 1993. Effects of caging juvenile predators on benthic infaunal populations at experimental open bay disposal areas in Galveston Bay, Texas. Report to Galveston District of the U.S. Army Corps of Engineers. National Marine Fisheries Service, Galveston Laboratory, Galveston, Texas, USA.
- Minello, T. J. and R. J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *Journal of Experimental Marine Biology and Ecology* **72**:211-231.
- . 1991. The role of estuarine habitats in regulating growth and survival of juvenile penaeid shrimp. Pages 1-16 in P. DeLoach, W. J. Dougherty and M. A. Davidson, editors. *Frontiers in shrimp research*. Elsevier Science Publishers, Amsterdam, The Netherlands.
- Minello, T. J., R. J. Zimmerman and E. X. Martinez. 1987. Fish predation on juvenile brown shrimp, *Penaeus aztecus*: effects of turbidity and substratum on predation rates. *Fishery Bulletin, U.S.* **85**:59-70.
- . 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. *Transactions of the American Fisheries Society* **118**:693-708.
- Minello, T. J., R. J. Zimmerman and R. Medina. 1994. The importance of edge for natant macrofauna in a created salt marsh. *Wetlands* **14**:184-198.
- Morris, J. T., B. Kjerfve and J. M. Dean. 1990. Dependence of estuarine productivity on anomalies in mean sea level. *Limnology and Oceanography* **35**:926-930.
- Nance, J. M. 1993. Gulf of Mexico shrimp fishery recruitment overfishing definition: workshop 2. NOAA Technical Memorandum, NMFS-SEFSC-323.
- Nance, J. M., E. F. Klima and T. E. Czaplak. 1989. Gulf of Mexico shrimp stock assessment workshop. NOAA Technical Memorandum, NMFS-SEFSC-239.
- Neill, C. and L. A. Deegan. 1986. The effect of the Mississippi River delta lobe development on the habitat composition and diversity of Louisiana coastal wetlands. *American Midland Naturalist* **116**:296-303.
- Nixon, S. W. 1980. Between coastal marshes and coastal waters—a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437-524 in P. Hamilton and K. B. Macdonald, editors. *Estuarine and wetland processes with emphasis on modeling*. Plenum Press, New York, New York, USA.
- Orth, R. J., K. L. Heck and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* **7**:339-350.

- Orth, R. J. and J. van Montfrans. 1982. Predator-prey interactions in a *Zostera marina* ecosystem in the lower Chesapeake Bay, Virginia. Pages 81-94 in R. J. Orth and J. van Montfrans, editors. Interactions of resident consumers in a temperate estuarine seagrass community: Vaucluse Shores, Virginia, USA. VIMS-SRAMSOE 267, Gloucester Point, Virginia, USA.
- Peters, D. S. and W. E. Schaaf. 1991. Empirical model of the trophic basis for fishery yield in coastal waters of the eastern USA. Transactions of the American Fisheries Society 120:459-473.
- Peterson, G. W. and R. E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17:235-262.
- Rabalais, N. N., F. R. Burditt, Jr., L. D. Coen, B. E. Cole, C. Eleuterius, K. L. Heck, Jr., T. A. McTigue, S. G. Morgan, H. M. Perry, F. M. Truesdale, R. K. Zimmer-Faust and R. J. Zimmerman. 1995. Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico Estuaries. Bulletin of Marine Science 57:855-876.
- Reed, D. J. and D. R. Cahoon. 1992. The relationship between marsh surface topography, hydroperiod and growth of *Spartina alterniflora* in a deteriorating Louisiana salt marsh. Journal of Coastal Research 8:77-87.
- Rejmanek, M., C. E. Sasser and J. G. Gosselink. 1987. Modeling of vegetation dynamics in the Mississippi River deltaic plain. Vegetatio 69:133-140.
- Rosas, C., E. Lazarochavez and F. Buckleramirez. 1994. Feeding habits and food niche segregation of *Callinectes sapidus*, *C. rathbunae* and *C. similis* in a subtropical coastal lagoon of the Gulf of Mexico. Journal of Crustacean Biology 14:371-382.
- Rozas, L. P. 1993. Nekton use of salt marshes of the Southeast region of the United States. Pages 528-537 in O. Magoon, W. S. Wilson, H. Converse and L. T. Tobin, editors. Coastal Zone '93, Volume 2. Proceedings of the 8th symposium on coastal and ocean management, American Society Of Civil Engineers, New York, New York, USA.
- . 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. Estuaries 18:579-590.
- Rozas, L. P. and D. J. Reed. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. Marine Ecology Progress Series 96:147-157.
- Rozas, L. P. and T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199-213.
- . 1998. Nekton use of salt marsh, seagrass and nonvegetated habitats in a South Texas (USA) estuary. Bulletin of Marine Science 63:481-501.
- Ruiz, G. M., A. H. Hines and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in nonvegetated estuaries - an example from Chesapeake Bay. Marine Ecology Progress Series 99:1-16.
- Ryer, C. H. 1987. Temporal patterns of feeding by blue crabs (*Callinectes sapidus*) in a tidal-marsh creek and adjacent seagrass meadow in the lower Chesapeake Bay. Estuaries 10:136-140.
- Sasser, C. E., M. D. Dozier, J. G. Gosselink and J. M. Hill. 1986. Spatial and temporal changes in Louisiana's Barataria Basin marshes, 1945-80. Environmental Management 10:671-680.
- Schindler, D. E., B. M. Johnson, N. A. Mackay, N. Bouwes and J. F. Kitchell. 1994. Crab:snail size-structured interactions and salt marsh predation gradients. Oecologia 97:49-61.
- Sullivan, M. J. and C. A. Moncreiff. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. Marine Ecology Progress Series 62:149-159.
- Thomas, J. L. 1989. A comparative evaluation of *Halodule wrightii* Aschers, *Spartina alterniflora* Loisel and bare sand as nursery habitats for juvenile *Callinectes sapidus* (Rathbun). Dissertation. Texas A&M University, College Station, Texas, USA.
- Thomas, J. L., R. J. Zimmerman and T. J. Minello. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. Bulletin of Marine Science 46:115-125.
- Turner, R. E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106:411-416.
- . 1997. Wetland loss in the northern Gulf of Mexico: multiple working hypotheses. Estuaries 20:1-13.
- Turner, R. E. and R. L. Allen. 1982. Bottom water oxygen concentration in the Mississippi River Delta Bight. Contributions in Marine Science 25:161-172.
- Turner, R. E. and Y. S. Rao. 1990. Relationships between wetland fragmentation and recent hydrologic changes in a deltaic coast. Estuaries 13:272-281.
- Turner, R. E., W. W. Schroeder and W. J. Wiseman. 1987. The role of stratification in the deoxygenation of Mobile Bay and adjacent shelf waters. Estuaries 10:13-19.

- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin, U.S.* 77:339-358.
- Wells, J. T. 1987. Effects of sea-level rise on deltaic sedimentation in South-central Louisiana. Pages 157-166 in D. Nummendel, O. H. Pilkey and J. D. Howard, editors. *Sea level change and coastal evolution*. The Society of Economic Paleontologists and Mineralogists, Tulsa, Oklahoma, USA.
- Wenner, E. L. and H. R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, USA, by postlarval and juvenile stages of *Penaeus* spp. (Decapoda, Penaeidae). *Journal of Crustacean Biology* 13:280-295.
- West, D. L. and H. Williams. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100:75-95.
- Whaley, S. D. 1997. The effects of marsh edge and surface elevation on the distribution of salt marsh infauna and prey availability for nekton predators. Thesis, Texas A&M University, College Station, Texas, USA.
- Wheeler, R. S. 1969. Culture of penaeid shrimp in brackish-water ponds, 1966-67. *Proceedings of the Southeast Association of Game and Fish Commissioners* 22:387-391.
- Wilson, K. A., K. W. Able and K. L. Heck. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Marine Ecology Progress Series* 58:243-251.
- Wilson, K. A., K. L. Heck and K. W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fishery Bulletin, U.S.* 85:53-58.
- Zimmerman, R. J. and T. J. Minello 1984a. Densities of *Penaeus aztecus*, *P. setiferus* and other natant macrofauna in a Texas salt marsh. *Estuaries* 7:421-433.
- 1984b. Fishery habitat requirements: utilization of nursery habitats by juvenile penaeid shrimp in a Gulf of Mexico salt marsh. Pages 371-383 in B. J. Copeland, K. Hart, N. Davis and S. Friday, editors. *Research for managing the nation's estuaries*. UNC-SG-84-08, UNC SeaGrant Publications, Raleigh, North Carolina, USA.
- Zimmerman, R. J., T. J. Minello, T. J. Baumer and M. C. Castiglione. 1989. Oyster reef as habitat for estuarine macrofauna. NOAA Technical Memorandum, NMFS-SEFC-249.
- Zimmerman, R. J., T. J. Minello, M. C. Castiglione and D. L. Smith 1990a. The use of *Juncus* and *Spartina* marshes by fisheries species in Lavaca Bay, Texas, with reference to effects of floods. NOAA Technical Memorandum, NMFS-SEFC-251.
- 1990b. Utilization of marsh and associated habitats along a salinity gradient in Galveston Bay. NOAA Technical Memorandum, NMFS-SEFC-250.
- Zimmerman, R. J., T. J. Minello, E. F. Klima and J. M. Nance. 1991. Effects of accelerated sea-level rise on coastal secondary production. Pages 110-124 in H. S. Bolton, editor. *Coastal wetlands*. American Society of Civil Engineers, New York, New York, USA.